

Seasonality of aquatic invertebrates in low-latitude and Southern Hemisphere inland waters

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Abstract

The seasonality of freshwater aquatic invertebrates in Southern Hemisphere and low-latitude inland waters in Africa, Australasia and South America is reviewed. Fauna from the tropics to temperate latitudes manifests some seasonality, the amplitude of which tends to increase, albeit inconsistently, with latitude. The wide diversity of habitats considered, and deficiencies in the data preclude generalizations about patterns and magnitude of seasonal response, which principally reflect system-specific events and interactions. For example, zooplankton declined after mixing events in some stratified systems, but increased in others, food availability being implicated. Zooplankton was most abundant in summer in some stratifying systems, and in winter in others, while in most non-stratifying systems, it was most abundant around the winter solstice, and in several, declined during the rainy season.

Seasonality of the zoobenthos was frequently linked to hydrological events such as fluctuations in water level which potentially influence food and habitat availability. Seasonal anaerobiosis in shallow sheltered waters and deeper hypolimnia imposes spatio-temporal restrictions on the benthic fauna. Low oxygen solubility, rapid oxygen depletion and decomposition of organic food matter at the elevated temperatures are probably significant influences. Life histories of Southern Hemisphere stream fauna appear seasonally flexible and opportunistic by contrast with the apparently synchronous cycles exhibited by north temperate representatives. Such flexibility may be selective both in respect of climatic unpredictability and equability.

The influences of predation and resource availability upon seasonal dynamics remain to be explored more fully, particularly in aquatic ecosystems in warm, arid regions which lack the climatic 'predictability' of the cooler, humid, temperate zones.

Introduction

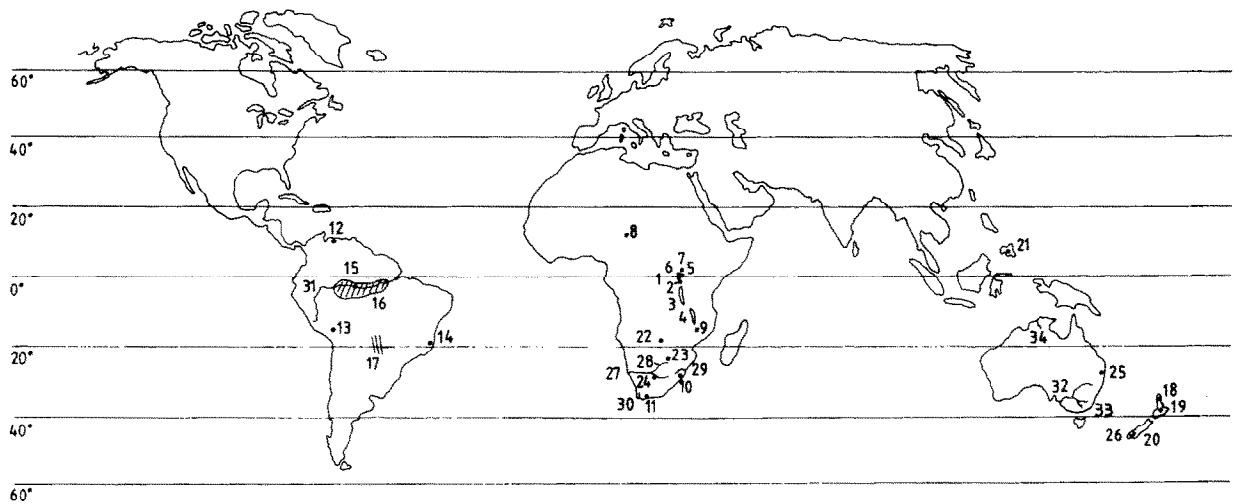
This contribution examines features of seasonality exhibited by aquatic invertebrates in some inland waters of the Southern Hemisphere (Fig. 1; Table 1). Seasonality is used here to refer to the property or feature of being dependent upon, related or restricted to, or varying with climatic seasons. Thus it embraces temporal behaviour with a periodicity or return period of one year or less. Certain studies undertaken in low-latitude waters in the Northern Hemisphere have also been included since compari-

sons between low and high latitudes are equally if not more meaningful than those based upon the artificial dichotomy between the Northern and Southern Hemispheres. While Southern Hemisphere inland waters are obviously not all tropical, the situation in tropical waters is particularly pertinent in this account.

In essence, the seasonal performance of faunal populations reflects the balance between birth and death rates. These are influenced as fundamentally by the bioenergetic processes of consumption, production and respiration (Grodzinski *et al.*, 1975) as

Table 1. Continued. Location and selected attributes of some ecosystems referred to in Fig. 3 & 9. Depth is given either as lake average, maximum, or study site. Mixing types: M = monomictic, D = dimictic, P = polymictic, U = unstratified. Annual temperature range approximate, to nearest degree. Trophic status: O, M, E, HE = oligo-, meso-, eu- and hyper-eutrophic. Zooplankton trends: Inc = increase, Dec = decrease. Annual range in abundance as settled volume (V), density (D) or biomass (B). Dominant or important zooplankton genera. Cyclopoida: Cyc = Cyclops, Euc = Eucyclops, Macro = Macrocyclus, Mesoc = Mesocyclops, Thermoc = Thermocyclops, Tropoc = Tropocyclops. Calanoida: Argyrod/iaptomus, Boeck/ella, Cal/amoecia, Diapt/omus, Lov/enula, Metad/iaptomus, Notod/iaptomus, Pseudod/iaptomus, Thermod/iaptomus, Tropod/iaptomus, Cladoceera: Bos/mina, Cerio/daphnia, Chyd/orus, Daph/nia, Diaph/anasma. Rotifera: Asp/lanchna, Bra/chionus, Con/ochilus, Cono/chiloidea, Fil/inia, Hex/arhra, Ker/atella, Poly/arhra Tri/choerica. Insecta: Chao/borus.

System (Country/Continent) *Reservoir	Depth	Latitude	Mixing type	Annual temperature range	Trophic status	Zooplankton response during stratification	Zooplankton response after circulation	Annual range in abundance	Dominant or major Zooplankters	Authority
Rotoiti (New Zealand)	59	38° S	M	11-19	O/M	Inc, Dec	Inc	9D	Cal, Macro, Bos, Cerio.	Chapman (1973)
Taupo (New Zealand)	97	38° S	M	11-22	O	Dec, Inc	Dec	14D	Boeck, Cerio, Bos, Macro, Poly, Con, Asp, Hex.	Forsyth & McCallum (1980)
Hayes (New Zealand)	33	45° S	M	6-20	E	Dec, Inc	Dec	6B	Boeck, Cerio, Bos, Daph, Chyd, Asp, Fil, Ker, Hex.	Burns & Mitchell (1980) Burns (1979)
Johnson (New Zealand)	27	45° S	M	7-20	E	Dec, Inc	Inc	25B	Cerio, Bos, Boeck, Macro, Euc, Chyd, Daph, Asp, Fil, Ker, Hex.	Burns & Mitchell (1980) Burns (1979)
CIRCULATING SYSTEMS										
George (Africa)	2	0°	U	23-30	E			2B	Thermoc, Mesoc, Cerio, <i>Moina</i> , Daph.	Burgis (1971, 1974)
Naivasha (Africa)	7	½° S	P	18-27	E			5B	Thermoc, Diaph, Bra, Mesoc.	Mavuti & Litterick (1981)
Albert (Africa)	25	1° N	U	28-29	O/M?			14D	Daph, <i>Moina</i> , Cerio.	Green (1971)
Chad (Africa)	3	13° N	P	17-31	M/E			9B	Tropod, Thermod, Thermoc, Daph, Bos, <i>Moina</i> .	Gras & Saint- Jean (1983)
Chilwa (Africa)	2	15° S	U	20-39	M/E			25D	Tropod, Diaph, Daph.	Kalk (1979a, b)
Sibaya (Africa)	30	27° S	U	18-28	O/M			13D	Pseudod, Bos, <i>Moina</i> , Mesoc, Thermoc, Tropoc.	Hart & Allanson (1975) Hart (1981a)
Groenvlei (Africa)	6	34° S	P/U	13-27	O/M			12D	Mesoc.	Coetzee (1980)
Rotorua (New Zealand)	10	38° S	P/U	10-20	M/E			7D	Cal, Bos, Cerio.	Chapman (1973)
Mahingerani* (New Zealand)	7	45° S	P	11-15	M/E			38D	Cerio, Bos, Boeck.	Mitchell (1975)



LAKES

1. EDWARD
2. KIVU
3. TANGANYIKA
4. MALAWI
5. GEORGE
6. NAIVASHA
7. ALBERT
8. CHAD
9. CHILWA
10. SIBAYA
11. GROENVLEI
12. VALENCIA
13. TITICACA
14. DOM HELVECIO
15. JACARETINGI
16. AMAZON BASIN LAKES
17. PANTANAL LAKES
18. OTOTOA
19. TAUPO, ROTORUA & ROTOITI
20. HAYES & JOHNSON
21. LANAO

RESERVOIRS

22. KARIBA
23. HARTBEESSPOORT
24. LE ROUX
25. NORTH PINE
26. MAHINGERANI

RIVERS

27. ORANGE
28. VAAL
29. PONGOLA
30. EERSTE
31. AMAZON
32. MURRAY DARLING
33. GOULBURN
34. ALLIGATOR

Fig. 1. Approximate global location of selected aquatic ecosystems referred to in the text.

they are by the population effects of predation, parasitism and disease, and both inter- and intra-specific competition, since maintenance of a positive energy balance is a clear prerequisite for survival, growth and reproduction.

Biotic and abiotic factors enforce simple numerical population changes and/or give rise to qualitative changes which lead to the replacement of one species by another. This feature of species succession is not necessarily a prerequisite for 'seasonality', but it exists widely as a seasonal response to changing biotic and/or abiotic conditions (Hutchinson, 1967; Sommer *et al.*, in press) and is especially conspicuous as the seasonal 'periodicity' exhibited by phytoplankton (Reynolds, 1984).

Temperature, the precise values and annual range of which vary with latitude (Straškraba, 1980), is a ubiquitous marker of seasonal change. It has profound direct influences upon many biotic

processes through its effects upon metabolism. Indirectly it controls many limnological events through its influence upon stratification and mixing. Consideration of the topic of faunal seasonality thus requires a rudimentary examination of thermal influences on aquatic invertebrates, followed by some discussion of the temporal influences of food availability and predation.

Thermal influences

Temperature influences aquatic invertebrates through a variety of direct and indirect mechanisms. Most directly, the thermal tolerance range of a species will regulate its geographical distribution (e.g. Hart, 1983) and possibly also its seasonal occurrence. Reproductive and emergence patterns of aquatic insects are affected by temperature (Van-

note & Sweeney, 1980) while through its direct influence upon metabolism, temperature modifies bioenergetic balances and growth.

Given the general increase of metabolic rate with temperature (e.g. Krogh's curve, Duncan & Klekowski, 1975) it is evident that seasonal temperature increases can potentially reduce the amount of energy available for growth and reproduction unless consumption and assimilation is increased commensurately. In *Ceriodaphnia reticulata* (Jurine) for instance, energy deficits which arise at elevated temperatures result in regular seasonal population declines (Gophen, 1976a). Conversely, specific catabolism and respiration is reduced with increasing temperature in *Mesocyclops leuckarti* (Claus). This permits a sufficient acceleration of development rates and egg production to offset the negative effects upon fecundity of smaller adult size and reduced longevity (Gophen, 1976b). The seasonal occurrence and abundance of these two species in Lake Kinneret is determined by their contrasting temperature-specific bioenergetic responses.

Inverse relationships between body size and water temperature have been widely observed in aquatic invertebrates, notably in sub-tropical and temperate copepods (Hart, 1981a; Burns, 1979). Fecundity tends to increase with body size (Hart, 1981a, b; De Moor, 1982), and is thus potentially enhanced at low temperatures, although this benefit is offset by the increase in embryonic development rate and potentially faster turnover of smaller clutches at elevated temperatures.

Temperature is frequently implicated as a causal factor in the seasonal behaviour of specific populations. Undoubtedly it plays a major rôle in this regard. However, temperature is also the most consistent signature of seasonality, and the association of underlying causal factors with it may cloud the determination of direct causality.

Nutritional influences

Direct food limitation is a powerful mechanism of population control within aquatic fauna (e.g. Hebert, 1982; Tessier & Goulden, 1982; Smith & Cooper, 1982). Within zooplankton, changes in size-specific fecundity, size-specific body carbon content (A. Duncan, Royal Holloway College, Lon-

don, pers. comm.) or lipid content (Tessier & Goulden, 1982), provide the clearest, but not always unequivocal, examples of food limitation. Size-specific fecundity, for example, can be influenced by differential predation rates linked to the conspicuousness of egg-bearing females, and to reductions in their escape capabilities.

Qualitative influences of nutrition upon community dynamics may be very subtle and selective. For instance, Gliwicz (1977, 1980) demonstrated the profound influence of large filamentous algae upon planktonic cladocerans. High densities of such filaments more adversely affect the ingestion rate and energy balance of large than small cladocerans (Porter & McDonough, 1984). Populations collapse and are replaced by other species better able to exploit prevailing conditions. Blooms of filamentous cyanophytes exert greater negative influences on zooplankton than colonial forms like *Microcystis* (Infante & Riehl, 1984), while cyanophyte-related toxicity can depress zooplankton filtration and incorporation rates below maintenance requirements (Porter & Orcutt, 1980). Benthic invertebrates may show marked preferences for leaves of particular tree species. This selectivity depends partly upon the nature and abundance of the colonizing decomposition microflora (Kaushik & Hynes, 1968; Bärlocher & Kendrick, 1973).

In essence, therefore, specific capabilities to acquire and utilize energy, which often vary with temperature, influence or determine competitive ability within the community. Susceptibility to predation (see below), is superimposed upon this; competition between congeneric cladocerans can depend interactively upon species-specific fecundity and escape responses (Jacobs, 1977a, b, 1978).

Predation influences

Predation frequently alters prevailing competitive balances, and thus drives species succession. The severity of its impact upon aquatic biota is evident from the observations of Brooks & Dodson (1965) on the local extinction of certain large species of zooplankters, following exposure to an unfamiliar predator. Two contrasting predation pressures affect zooplankton (O'Brien, 1979; Zaret, 1980). Generally, visual predation by vertebrates selectively removes large conspicuous elements

lacking adequate suction-avoidance responses, while tactile predation by invertebrates focuses upon small prey species.

Opportunities for foraging by visual predators during summer will be lower in low- than in high-latitude waters because of relatively shorter day-lengths. Visual predation is influenced adversely by a reduction in reactive distance (Vinyard & O'Brien, 1976). The high levels of inorganic turbidity which occur in many waters in arid or semi-arid Southern Hemisphere regions (Kirk, Bruton, this volume) accordingly facilitate the co-existence of large zooplankters with their visual predators (Hart *et al.*, 1983; Geddes, 1984).

Some considerations of low-latitude waters

Tropical lakes are generally characterized by small seasonal variations in water temperature; despite earlier notions to the contrary, they do not necessarily lack seasonality (Lewis, 1979; Serruya & Pollinger, 1983). It is recognized that climatic factors other than solar radiation effect seasonal change. Rainfall and wind (Talling, 1966; Beadle, 1974; Lewis, 1979; Twombly, 1983; Serruya & Pollinger, 1983) are frequently markedly seasonal in the tropics, and serve as effective determinants of seasonality. Noting the limited seasonal variation in irradiance in the tropics, Beadle (1974) drew attention to the greater potential rôle of nutrients to serve as the primary growth-limiting factor for algae (and hence higher trophic levels) at low latitudes.

Imberger (this volume) has demonstrated a high stability in thermal stratification patterns in low-latitude Southern Hemisphere waters. Conversely, slight reductions in temperature may suffice to destabilize warm water bodies, and tropical lakes are susceptible to temporary non-seasonal or episodic disturbances following wind- or rainfall-induced cooling events. By contrast, the greater stability of temperate lakes during summer stratification minimizes the influence of sporadic weather changes upon their regular seasonal pattern (Lewis, 1979). Thus tropical and temperate lakes may differ radically in their seasonal predictability. Stratified waters at intermediate latitudes (between c. 20° and 30°) possess an extreme stability potential as a result of the relatively high absolute temperatures and

the large vertical thermal gradients which develop (Serruya & Pollinger, 1983).

Seasonality of zooplankton

A schematic outline of factors which contribute interactively to the seasonality of limnetic zooplankton communities is shown in Fig. 2. In seasonally extreme environments, annual pioneer populations which arise from inocula can increase at a rate which depends upon the magnitude of the positive energy balance and the stock of breeding adults; temperature, food quantity and quality, and organism size are important. Proliferation of this population through potential exponential growth over-exploits available resources, and negative feedback, which may be compounded by the concurrent or subsequent developments of predator, parasite, or competitor populations, is imposed.

Species better able to tolerate depressed food conditions, to use different food species, or less vulnerable to prevailing predation pressures tend to replace the seasonal pioneer, resulting in succession. Following formulation of the Size-Efficiency Hypothesis (Brooks & Dodson, 1965) and its critical evaluation (Hall *et al.*, 1976), it is recognized that succession may involve other factors (Kerfoot, 1980).

Zooplankton is frequently dominated by microphagous herbivores, whose seasonality is partly influenced by the availability of phytoplankton food. Accordingly, seasonal dynamics of the zooplankton are usefully addressed by reference to two types of waters, arrayed latitudinally. Firstly, lakes and reservoirs deep enough or sufficiently sheltered to develop stable seasonal thermal stratification, and secondly, those sufficiently shallow or exposed to ensure continuous or nearly continuous circulation. Flowing waters with intermittently flooded off-channel basins, and temporary waters constitute two additional biotopes. The latter is not considered further here (cf. Williams, this volume).

Zooplankton seasonality in stratified waters

The effective underwater light climate and availability of nutrients for phytoplankton growth are influenced by circulation patterns. Despite contin-

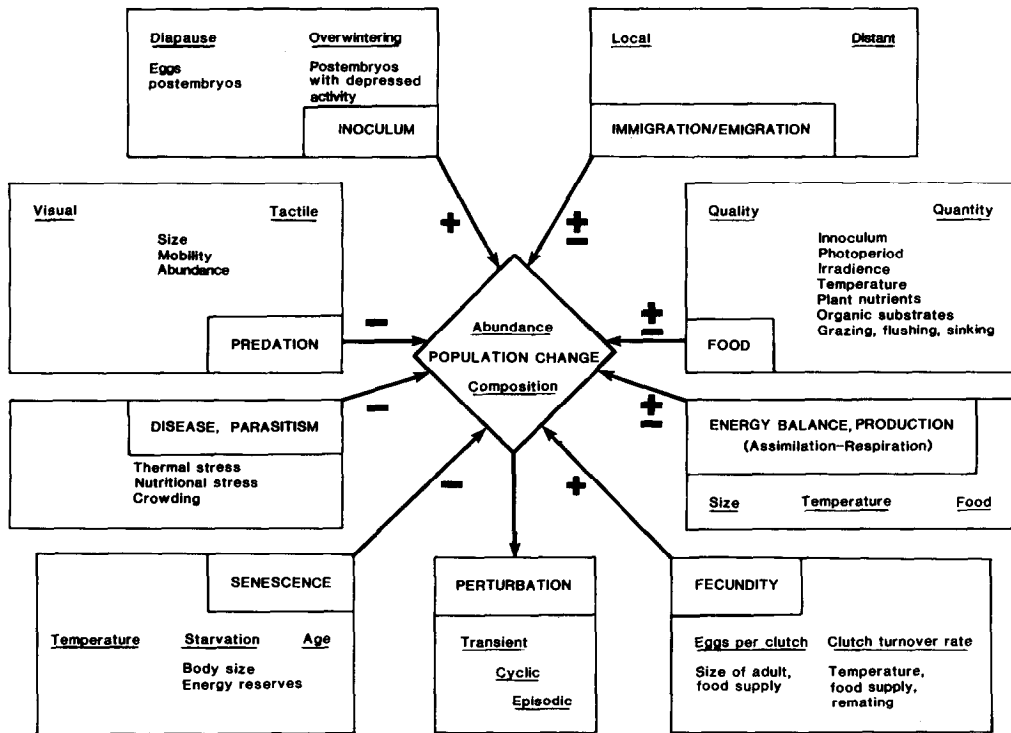


Fig. 2. Factors influencing the seasonality of aquatic invertebrates, with particular reference to the zooplankton.

ously adequate insolation, phytoplankton growth in deep tropical lakes may be depressed by light-limitation during deep-mixing events. Conversely, mixing also serves to recycle nutrients and to stimulate algal growth, if light is not concurrently limiting (Lewis, 1979; Twombly, 1983). The duration of such mixing events is crucial. Transient, aperiodic events may be survived by algae and zooplankton drawing upon stored energy reserves. More prolonged mixing, characteristic of regular annual circulation events, is more likely to result in collapse of the plankton populations.

Generation times of zooplankters range from days in the case of rotifers and small cladocerans, through several weeks in larger cladocerans and small copepods, to many weeks or months in large copepods (Allan, 1976). Development times generally decrease with temperature so that response times may be quite rapid in warm waters, allowing smaller zooplankters especially to exploit transient opportunities.

Fig. 3 illustrates seasonal changes in zooplankton standing stock (ZSS) in a variety of stratifying

waters in the Southern Hemisphere and in some low-latitude waters in the Northern Hemisphere. Seasonal responses in ZSS in these stratified systems are highly variable. During stratification, ZSS generally increased in seven lakes (10–>200 m in depth), decreased in another seven (15–110 m), and remained almost stable in three (30–60 m) (Table 1). Following mixing, ZSS tended to increase in thirteen lakes (10–>200 m) and to decrease in four (24–100 m). Unimodal, bimodal and multimodal annual patterns in ZSS were evident (Fig. 3). Differences in the complexity of the seasonal variations are variously attributable to the temporal resolution of the sampling programme, to the taxonomic treatment of the samples (monospecific or total community analyses), and to whether numerical or gravimetric estimates of ZSS were used.

The data reveal the existence of summer maxima in some systems, and winter maxima in others within the corresponding latitudinal range. There is also no uniform or consistent relationship between the amplitude of seasonal variation and latitude (Fig. 4). Annual variation is frequently as marked in

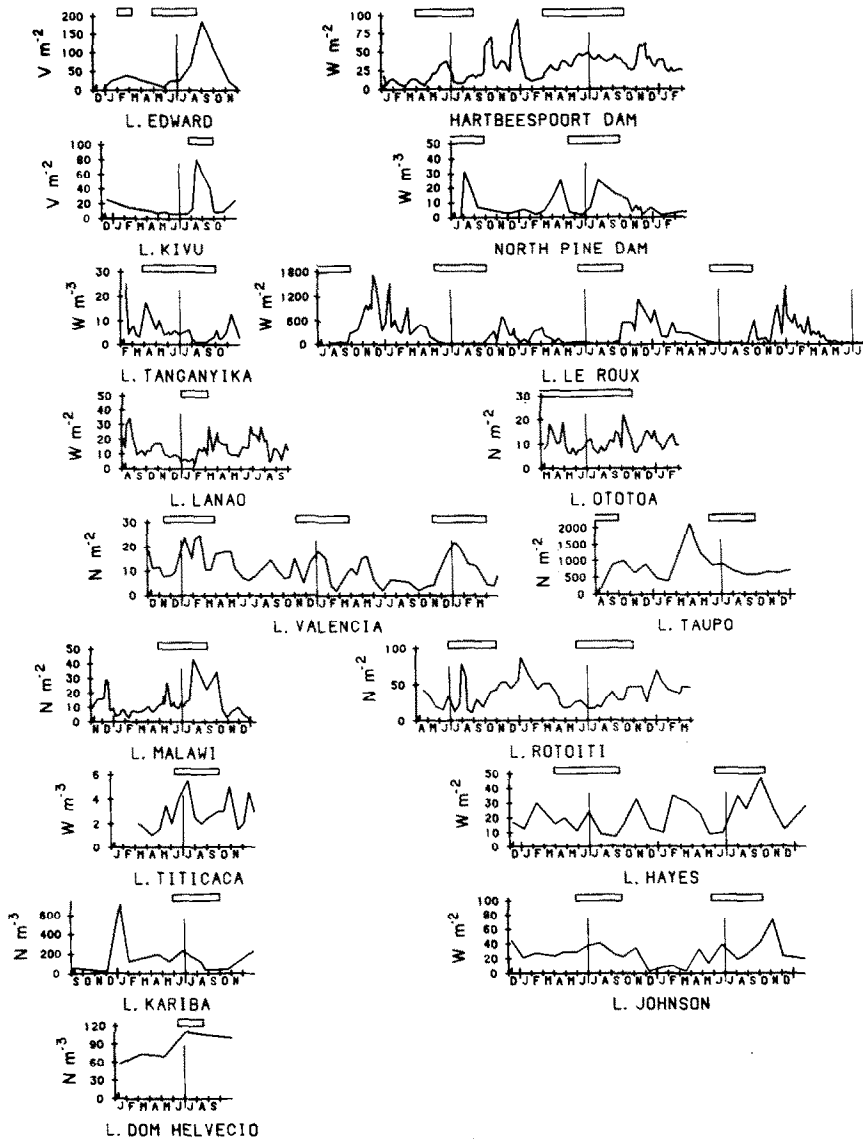


Fig. 3. Seasonal variation in abundance of zooplankton in low latitude and Southern Hemisphere lakes and impoundments which stratify seasonally. Ordinates are relative scales of biomass (W), density (N) or settled volume (V) per unit area (m^{-2}) or per unit volume (m^{-3}). The winter solstice is shown by the vertical lines. Periods of circulation are indicated approximately by the horizontal bars. Authorities for the data portrayed, and further details of the water bodies are given in Table I. Fig. 1 gives most site locations.

tropical and subtropical systems as it is in temperate waters (e.g. compare Lakes Edward ($0.5^{\circ}S$) and Johnson ($45^{\circ}S$)). No consistent seasonal pattern or generalized scheme of succession and periodicity of the type derived for phytoplankton (Reynolds, 1982, 1984) is evident for the zooplankton at this level of analysis. Patterns reflect the system-

specific responses of particular species or communities to the particular limnological features of the system, as far as can be judged. Fuller descriptive accounts of seasonal events in a number of water bodies (Fig. 3) are given below. The terms spring, summer, autumn and winter are used for convenience in describing consecutive quarters of the

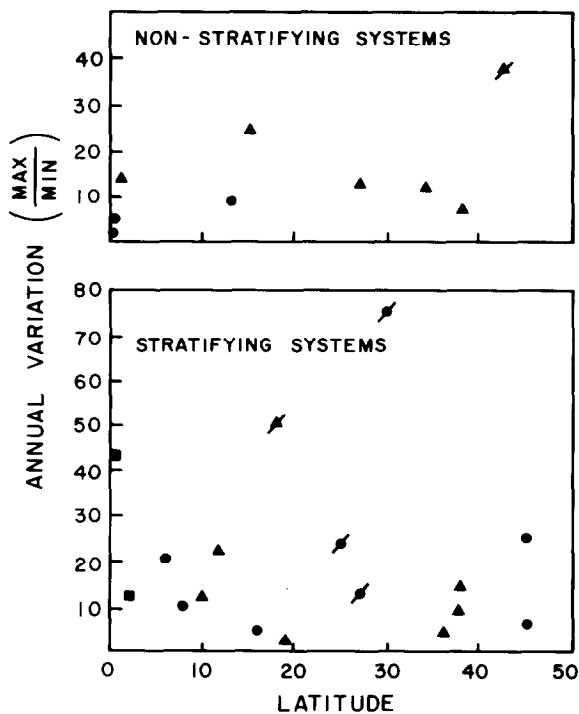


Fig. 4. Annual variations in zooplankton abundance (ratio of maximum to minimum) as a function of latitude for lakes and reservoirs indicated in Table 1, in terms of biomass (●), density (▲), or settled volume (■). Reservoirs are marked (-).

annual cycle even where such seasonal differentiation is regionally inappropriate.

Bimodal changes in ZSS were observed in Lake Edward (0.5°S) during 1953 (Beadle, 1974; Seruya & Pollinger, 1983, after Verbeke, 1957). The major spring peak, largely of Cladocera, followed a phytoplankton increase stimulated by turnover. The subsequent late summer peak developed from a summer low after partial mixing; its subsequent collapse possibly resulted from the upwelling of anoxic water. Zooplankton in Lake Kivu (2°S) showed a similar pattern in which the major spring increase occurred during the windy period, possibly following nutrient-stimulated increases in algal production (Beadle, 1974). This peak, predominantly of Cladocera, declined rapidly as stratification progressed (Verbeke, 1957, cited by Mahy, 1979), and appears to have been followed by a secondary mid-summer peak.

Clear seasonal phases have been observed for phytoplankton and micro-zooplankton in Lake Tanganyika ($3\text{--}9^{\circ}\text{S}$), although no data exist for entomostracans (Hecky & Kling, 1981). Planktonic

Protozoa declined from a late summer/autumn peak to a spring low, and increased marginally in early summer. The major decline coincided with the windy, dry period between April and September (Beadle, 1974) when algal biomass was increasing (Hecky & Fee, 1981).

The major seasonal decline of zooplankton in Lake Lanao (8°N) coincided with the period of annual circulation during which phytoplankton growth became light-limited by deep-mixing and reduced insolation (Lewis, 1979). Rotifers and cladocerans (Allan's, 1976) *r*-selected species were more severely affected than copepods, whose larger size conferred upon them a greater tolerance of low food levels as a result of their lower specific metabolic rate and potentially greater energy reserves (Threlkeld, 1976). Many other, apparently erratic fluctuations in ZSS reflect transient perturbations (irregular calm and windy periods) leading to the formation or destruction of secondary thermoclines within the epilimnion (atelomixis) which influence phytoplankton stocks. Herbivore abundance in Lake Lanao correlated with certain key algal species. Predation by *Chaoborus* accounted for most of the observed mortality of zooplankton. Food quality was implicated as the major mortality factor for rotifers which were not significantly preyed upon by *Chaoborus*, the major target of fish predation.

Infante (1982) observed a recurrent annual cycle of ZSS in Lake Valencia (10°N). Nutrient remobilization and increased algal production after mixing stimulated the major annual abundance peak in winter. A secondary spring peak coincided with increases in nutrient availability at the start of the rainy season and the onset of stratification. Predation by juvenile fish resulted in a fairly consistent summer minimum in June, and zooplankton recovered during autumn. Toxicity-related mass mortalities of both fish and zooplankton occurred after full circulation (Infante *et al.*, 1979), but recovery to the annual winter peak was rapid. During these studies, the historically-dominant copepod *Notodiaptomus venezolanus* Kiefer was replaced by the smaller *Mesocyclops crassus* Fischer which appeared more tolerant of the prevailing extreme physico-chemical conditions, and is probably less vulnerable to visual predation. Three cladoceran species were displaced following an extraordinary increase of filamentous cyanophytes which adversely influenced their feed-

ing capabilities (Infante & Riehl, 1984).

Studies both in the central (12° S, Degnbol & Mapila, 1982) and southern (14° S, Twombly, 1983) sectors of Lake Malawi (9–14° S) have shown clear evidence of seasonality in zooplankton populations. Twombly (1983) observed large seasonal maxima during winter, while numbers were low during summer. The maxima of certain zooplankters coincided with the seasonal cycle of mixing, nutrient redistribution and algal proliferation. For others, repeated spring peaks occurred with the onset of stratification of the mixolimnion. Declines from subsidiary summer peaks may reflect trophic stagnation during the calm summer months. As in Lake Lanao, irregular episodic meteorological events interrupt underlying trends and introduce significant inter- and intra-annual variations which confound any latent seasonal regularity.

Seasonal changes in ZSS and other limnological variables were small in Lake Titicaca (16° S, 3 800 m a.m.s.l.) (Widmer *et al.*, 1975; Richerson *et al.*, 1975). Zooplankton stocks were highest in winter, following a phytoplankton peak in May. In Lake Dom Helvecio (19° S) bimonthly sampling (Matsumura-Tundisi & Okano, 1983) suggested a winter peak in copepod density, following breakdown of stratification. The dominance of copepod nauplii at that time implied a surge of reproductive activity.

A series of reservoirs constitutes the principal data base for thermally stratifying waters between 16° and 30° S. In Lake Cahora Bassa (16° S), monthly fluctuations in ZSS were directly linked to rhythmic changes in visual predation at night associated with the lunar cycle (Gliwicz, 1984). A preliminary account of the crustacean zooplankton in Mwenda Bay, Lake Kariba (19° S) suggested a numerical decline during spring to an early summer low, and subsequent rapid recovery to a mid-summer high (Mills, 1977). The winter decline followed the annual circulation period identified by Coche (1968, cited in Beadle, 1974), and the attendant increase in mixing depth and, presumably, depressed algal growth.

Zooplankton in hypertrophic Lake Hartbeespoort (25° S) did not show a regular cycle. Standing stocks were generally highest in early summer, while a less pronounced late autumn/early winter increase followed annual circulation (Seaman, 1977; A. Jarvis, National Institute for Water Research, Pretoria, pers. comm.) Similarly in North

Pine Reservoir (27° S) a late winter/early spring increase followed annual circulation (King, 1979). This peak declined as stratification progressed, and epilimnetic volumes were reduced by the upward extension of anoxic waters. Summer biomass was low, notwithstanding a seasonal phytoplankton peak at this time, suggesting that food quality may have been inferior. A major autumn peak followed massive inflows which raised the water level by c. 15 m in the final filling stages of this reservoir, and conceivably increased food supplies directly (by introducing allochthonous organics), or indirectly (by carrying plant nutrients). The resulting peak in ZSS declined with the breakdown of stratification.

The species succession of zooplankton over six years in Lake Le Roux (30° S) was reasonably consistent with, and predictable in terms of water temperature (Fig. 5). Very low standing stocks occurred during late autumn/winter. Biomass increased markedly in spring, with the onset of surface warming, to reach an early summer peak. In some years a secondary late-summer peak followed a mid-summer decline. In others, the first peak gradually declined to the winter lows. Temperature, in combination with water transparency and chlorophyll concentration, accounted for much of the observed overall variation in ZSS (Fig. 6), while annual mean ZSS levels were strongly correlated with heat content (Fig. 7). Differences in the specific composition of the daphnid assemblage in the

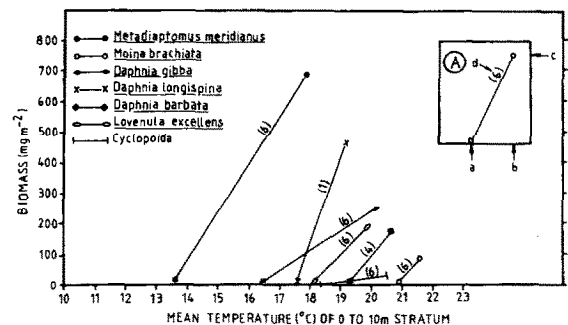


Fig. 5. Seasonal succession patterns of zooplankton in Lake Le Roux standardized with respect to mean water temperature. The key inset (A) shows: (a) average temperature at which the annual increase begins, (b) average temperature at which the annual biomass maximum is reached, (c) the mean maximum biomass attained by the species during years present and (d) the number of years the given species was a significant component of the plankton.

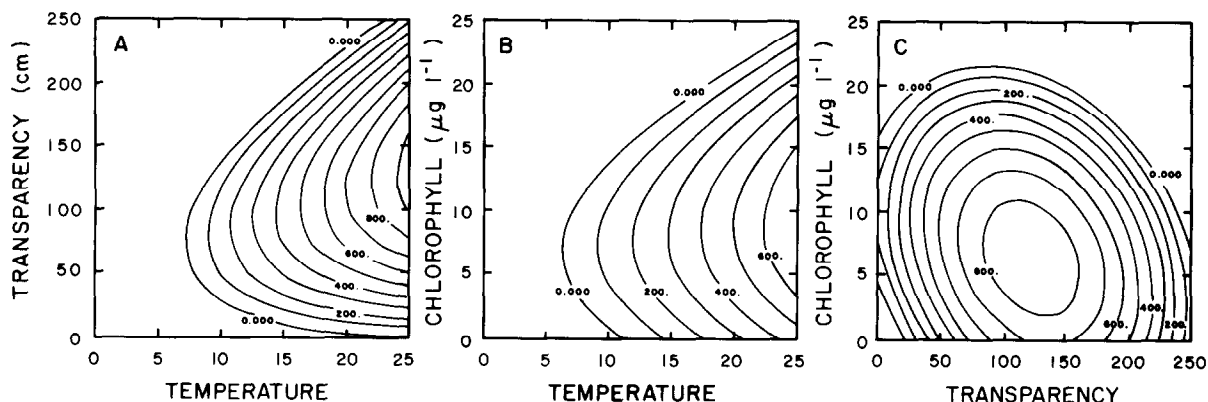


Fig. 6. Response surface plots of total zooplankton abundance in Lake Le Roux. The contours show zooplankton biomass predicted by multiple linear regressions as functions of two independent variables: (A) temperature and transparency, (B) temperature and chlorophyll concentration, (C) transparency and chlorophyll concentration.

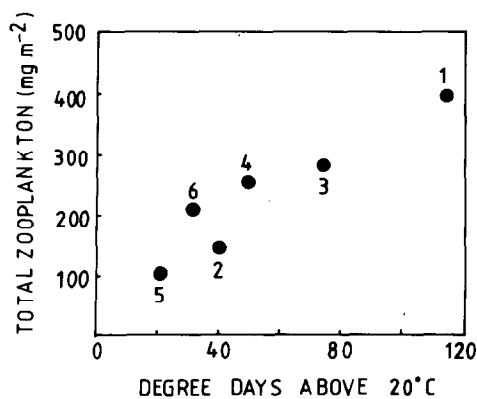


Fig. 7. Weighted annual mean zooplankton standing stocks in Lake Le Roux between 1977-78 (denoted as 1) and 1982-83 (denoted as 6) in relation to the number of degree-days above 20 °C in each hydrographic year (August-July).

system were related to transparency characteristics (Hart *et al.*, 1983).

A number of detailed zooplankton studies exist for waters between 36° and 45° S in New Zealand, where climate is tempered by maritime influences (Jolly & Brown, 1975). In Lake Ototoa (36° S) total ZSS fluctuated little, but exhibited clear peaks and troughs (Green, 1976). A spring peak of rotifers followed the onset of stratification; copepods and cladocerans gave rise to an autumn peak. In all, seven peaks were evident, many reflecting the proliferation of single species within the community. Many peaks were preceded by or coincided with increases in ingestible phytoplankton. Food-limita-

tion was inferred from Green's (1976) demographic analysis of *Calamoecia lucasi* Brady which demonstrated very low fecundity, low production rates and low *P/B* coefficients. In Lake Rotoiti (38° S) sequential species maxima resulted in several density peaks from spring to autumn (Chapman, 1973). In general, densities were highest in summer. The dominant zooplankter, *C. lucasi*, bred continuously and peaked recurrently. Food supply was considered to be important. At corresponding latitude, Forsyth & McCallum (1980) observed a spring/summer maximum in crustacean zooplankton density and a pronounced rotifer peak in autumn in Lake Taupo (39° S).

A bimodal annual cycle in ZSS occurred in Lake Hayes (45° S) (Burns & Mitchell, 1980). Spring/early-summer and late-summer peaks were separated by mid-summer and winter minima. The spring peak collapsed with the onset and progression of thermal stratification, but the second peak developed under stratified conditions. Primary production and algal standing stock showed a single annual peak in summer (Mitchell & Burns, 1981). The coincidence of a zooplankton minimum with the phytoplankton peak reasonably reflects the adverse qualitative influence, especially of *Anabaena*, upon zooplankton feeding. In a later study, peak densities of *Ceriodaphnia* or *Asplanchna* were recorded in mid-summer, but the overall pattern was broadly comparable with the preceding situation (Burns, 1979). Birth rates of *Boeckella dilatata* Sars were correlated with temperature and

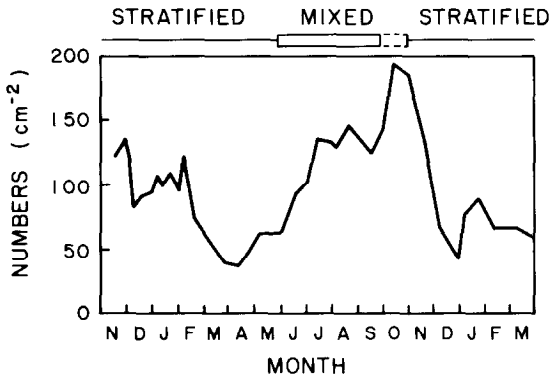


Fig. 8. Abundance of *Boeckella dilatata* Sars in relation to stratification and mixing patterns in Lake Hayes. (After Burns, 1979).

algal abundance, suggesting their dual influence on populations of this calanoid, whose densities consistently increased during circulation, and declined with the progression of stratification (Fig. 8). In nearby Lake Johnson (45 °S), Burns & Mitchell (1980) observed zooplankton peaks in winter with variable summer peaks either larger or smaller than the winter peak. As in Lake Hayes, zooplankton tended to increase during circulation and decline as stratification progressed, although secondary fluctuations obscured the trend. In contrast to Lake Hayes, late summer peaks were insignificant in Lake Johnson.

Zooplankton seasonality in circulating waters

Many shallow water-bodies circulate almost continuously or develop diel rather than seasonal stratification, often with favourable consequences for sustained primary production. Surface area to volume ratios of shallow systems are relatively high, allowing water levels in shallow endorheic basins to fluctuate widely as the balance between hydrologic inputs and evaporative or seepage losses varies. In exorheic systems, flushing times tend to vary instead.

Seasonal changes in ZSS in waters lacking stable seasonal stratification are shown in Fig. 9. Patterns of various complexity are evident, but with the seeming exception of Lake Naivasha (0.5 °S), seasonal lows in ZSS occur around the winter solstice. However, specific components of the com-

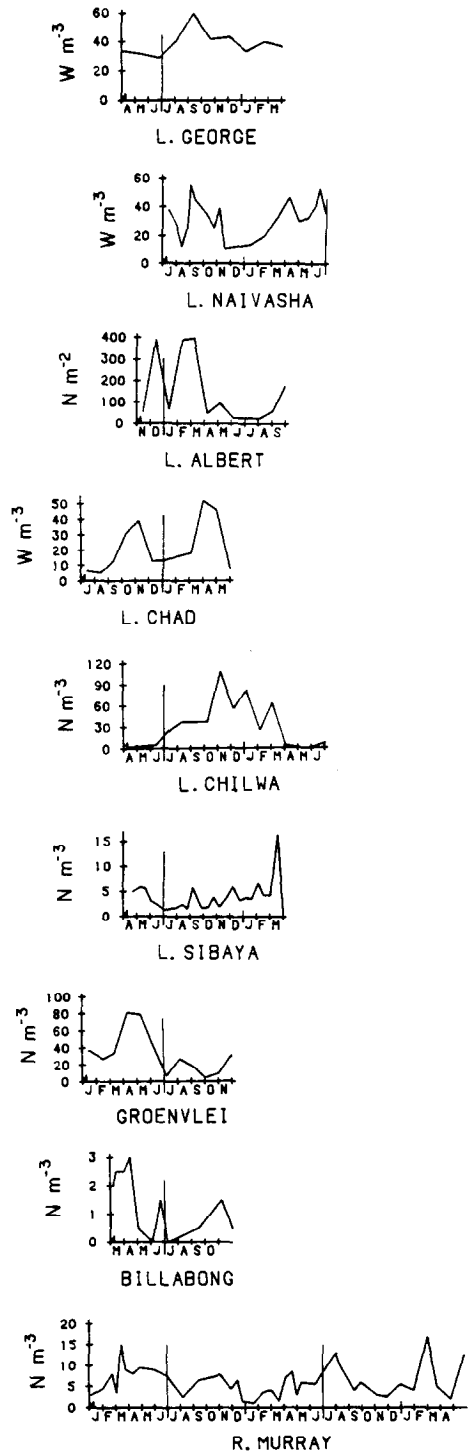


Fig. 9. Seasonal variation in abundance of zooplankton in poly-mictic or unstratified standing waters and the Murray River. For further details see legend to Fig. 3.

munity may exhibit winter maxima, as in Lake Rotorua (38 °S). The amplitude of seasonal change in ZSS is variable, and bears no consistent relationship to latitude (Fig. 4).

In several shallow systems, the abundance patterns of zooplankton appear to be influenced by the hydrological régime. Increases in ZSS during the dry season and decreases during the rainy season were recorded in Lakes George, Chad and Chilwa, while a converse trend was reported for Lake Naivasha. The relationships are seldom unequivocal since changes in water level and temperature are seldom seasonally independent. Dilution in endorheic basins, or increased washout in exorheic systems can decrease zooplankton populations (or their food resources) during the rainy season. Conversely, given the potential for nutrients to exert the major limitation to phytoplankton growth under conditions of sustained irradiance (Beadle, 1974), nitrogen-rich rainfall, or runoff carrying plant nutrients and allochthonous organics should serve to increase the food for consumers, either directly or after a lag period. The nature of the introduced organics (the size spectrum of the particulates, or the lability of dissolved compounds, etc.) and the turbidity of the nutrient-carrying waters are factors likely to influence the length of this lag. But at present the causal mechanisms underlying the observed zooplankton-hydrology relationships remain conjectural and are likely to differ depending upon site-specific features. For instance, swamp-ringed waters like Lake Chilwa are likely to differ from systems lacking this potential energy source. Specific descriptions of zooplankton seasonality in various circulating systems follow; selected examples are illustrated in Fig. 9.

The seasonal constancy of equatorial Lake George, around which much discussion of the stability of tropical lakes has revolved, is attributable to a number of its rather unique features, rather than reflecting a general characteristic of tropical lakes (Viner & Smith, 1973; Beadle, 1974; Burgis, 1978). Crustacean ZSS varies about two-fold in a roughly half-yearly cycle in this lake (Burgis, 1971; 1974). It increases during the dry season, and declines during the ill-defined rainy season. Viner & Smith (1973) commented on the high incidence of climatically-induced physical disturbances of the water column. Seemingly these perturbations are not translated into biotic responses, possibly be-

cause of their ephemerality. But in short-term studies over one week, Burgis (1971) reported two-fold variations in abundance of *Thermocyclops hyalinus* (Rehberg); these match the magnitude of annual variation. Despite depressed seasonality, significant short-term variations arise, presumably in response to aperiodic abiotic events, which assume equal or greater importance than seasonal events (Burgis, 1978).

In Lake Naivasha (0.5 °S), Mavuti & Litterick (1981) recorded fairly pronounced fluctuations in ZSS. These declined during the dry season (cf. Lake George) and bimodal peaks were evident during the rainy season. In Lake Albert (1 °N), which generally circulates despite its mean depth of 25 m, cladoceran densities underwent a major seasonal change. A bimodal summer peak in mid-lake densities (Green, 1971) declined markedly to a sustained minimum with the onset of the rainy season, a period when violent windstorms may induce complete mixing. The decline was conceivably mediated by a depression of algal production by deep mixing in this rather turbid system. Verbeke (1957), cited in Serruya & Pollinger (1983), found a converse seasonal pattern, with continuously high ZSS during the rains and low values during the dry seasons. This disparity may reflect the consistent differences in the faunal assemblages of in-shore and mid-lake regions which arise as a result of predation and competition mechanisms (Green, 1967, 1971).

Despite its relatively low latitude, Lake Chad (13 °N) shows fairly pronounced seasonal temperature variations. Zooplankton was generally most abundant during the warmer months (Robinson & Robinson, 1971; Gras & Saint-Jean, 1983). In the high water period of 1964/65, Gras & Saint-Jean (1983) found a bimodal biomass peak, with the increase to the April maximum coinciding with falling water levels and rising temperatures. The increase to the November maximum coincided with rising water levels and falling temperatures. In Lake Chilwa (15 °S), zooplankton densities also increased during summer and remained high into the cool autumn as water levels rose (Kalk, 1979a, b). Certain disruptions to the underlying trend were ascribed to changing predation patterns associated with the movement of breeding fish into surrounding swamps, and their subsequent return along with juveniles into the open waters.

Lake Sibaya (27 °S) is a deeper system which

circulates continuously. Its dominant calanoid bred year-round, and demonstrated a relatively constant population structure, apart from a relative increase of adults during summer (Hart & Allanson, 1975; Hart, 1981a). In general, population densities were highest during late spring/early summer and late summer/autumn, and were slightly depressed during the windiest period (mid-summer). An inferred increase in cyclopoid predation on the calanoid (Hart, 1981a) and/or a decrease in algal food associated with deeper mixing and lower insolation during this cloudy rainy period (Allanson, 1979) could have contributed to this summer decline.

In Groenvlei (34 °S), which is very shallow and well mixed by year round winds, Coetsee (1980) recorded minor zooplankton peaks in spring and autumn, a major summer peak, and barely detectable winter stocks. The autumn increase followed a late summer phytoplankton peak. In waste stabilization ponds (Gumeracha, 35 °S) in Australia, Mitchell & Williams (1982a, b) recorded an annual cycle with cool season maxima (around 12–15 °C) for *Daphnia carinata* (King); peaks occurred in autumn and late winter/early spring. Other species exhibited summer maxima, or occurred year-round. *Daphnia carinata* was considered to be food-limited at high population densities.

Entomostraca were perennial in Lake Rotorua (38 °S). Some species exhibited summer peaks, others winter peaks, and *Calamoecia* was present in significant numbers and bred year-round (Chapman, 1973). Despite their different stratification patterns, neighbouring Lakes Rotorua and Rotoiti exhibited similar annual patterns. At slightly greater latitude, zooplankton in polymictic Lake Mahingerani (45 °S) was more strongly seasonal, with clear winter minima, and spring and mid-summer peaks. Changes in ZSS tracked phytoplankton production curves reasonably (Mitchell, 1975).

Zooplankton seasonality in rivers and floodplain lakes

Off-channel floodplain lakes (pans, billabongs, etc.) associated with lotic systems rely upon hydrological events for their maintenance. In South America, Matsumura-Tundisi & Okano (1983) noted that while ZSS was highest at low water levels both in Amazonian river-lakes (0–10 °S) and the

Pantanal lake system (c. 20 °S), these maxima occurred during wet and dry seasons, respectively. They suggested that water level rather than rainfall itself was the controlling influence, and interpreted ZSS peaks at low water level as lagged responses to the enrichment of flood-plain lakes by allochthonous inputs carried by the flood-waters. Conversely, in Lake Jacaretinga (3 °S), ZSS decreased 100-fold in the month preceding Amazonian inflows while a 25-fold increase during the floods collapsed almost totally within a month (Brandorff & de Andrade, 1978). The decline was ascribed to dilution, flushing and predation by immigrant breeding fish.

Flood-waters often carry high inorganic suspended loads, which are known to influence the feeding capabilities of some temperate cladocerans adversely (Arruda *et al.*, 1983; McCabe & O'Brien, 1983), in addition to detracting from the optimal light climate for photosynthesis. Yet the increased body size of a calanoid and increased fecundity of a cladoceran following inputs of Amazonian flood-waters (Brandorff & de Andrade, 1978) imply an improved rather than impoverished food environment, and/or a decrease in competition associated with the decline in ZSS. Striking increases in heterotrophic activity following a rise in water level in such lakes (Rai & Hill, 1981) potentially improve trophic conditions for microphagous filter-feeders. Organic matter adsorbed onto clay particles carried in flood-waters represents a potentially significant energy resource for filter feeders able to exploit it (Arruda *et al.*, 1983).

Lentic floodplain environments may receive significant seasonal energy pulses following the inundation of fringing terrestrial vegetation, in addition to any allochthonous material carried by the flood-waters themselves e.g. the Pongola River floodplain pans (27 °S) whose fauna respond to these seasonal inputs (Heeg & Breen, 1982). As in the Amazonian 'várzea' lakes, the terrestrial vegetation which partly drives the aquatic system is itself dependent upon nutrients deposited by the preceding floods. The effects of inundation may be slight, however. Shiel (1976) concluded that the fauna of a Goulburn River Billabong (37 °S) was scarcely influenced by inundation, despite considerable through-flow. A mid-winter peak of the pelagic Crustacea associated with hydrophyte beds arose, possibly in response to the transformation of frag-

ments stemming from seasonal macrophyte die-back into detritus particles small enough to be utilized.

Despite considerable interest in river zooplankton, especially in Australia (Shiel, 1981; Shiel & Koste, 1983; Koste & Shiel, 1983), little is known about its seasonality in Southern Hemisphere rivers. In a study of the lower Murray River, Shiel *et al.* (1982) recorded lowest zooplankton densities during winter/early spring and highest densities in summer/autumn. Temperature, turbidity and salinity were implicated in the seasonal succession of this community. The relative contributions of episodic inflows from the slightly regulated Darling River and the more continuous flows from the strongly regulated upper Murray River determined the species composition of the zooplankton. Riverine rotifers predominated in the former, while more typical limnetic Entomostraca arose from the latter. Seasonal cycles of the potamoplankton were seen to be less distinct than those reported for rivers in the Northern Hemisphere, where seasonal regularity may be imposed by greater environmental predictability.

Some conclusions

It is clear from the above that seasonality exists within the zooplankton in some Southern Hemisphere and tropical waters. Extension from this largely descriptive account to an interpretative assessment is thwarted by the limited depth of understanding available for most of the case studies.

A sequential model of planktonic seasonality (the PEG-model) developed largely around a Northern Hemisphere data base (Sommer *et al.*, in press) envisages succession and its associated seasonality as basically predictable and directional. Physical factors are considered to exert deterministic influences largely at the beginning of spring and towards the end of autumn. The principal determinants of succession during the growing season are considered to be biological interactions, especially predation and food limitation. Few of the studies considered in the present account are sufficiently analytical to assess the validity of the PEG-model. Studies on Lakes Lanao and Malawi, for example, lend credence to the applicability of the PEG-model postulates. In these two systems at least, the reduc-

tion in stability of stratification provides the opportunity for physical events to punctuate an otherwise predictable sequence not shared by systems which stratify stably. Physical factors strongly influence seasonality, but parallel deterministic influences of direct biological effects and interactions undoubtedly exist; the influence of food availability and of algal growth – zooplankton grazing interactions; the influence of predation and its feed-back upon zooplankton abundance and composition, etc. Several examples involve such mechanisms, but quantify them poorly or not at all. The extended growing season at lower latitudes afford greater opportunities for biotic factors to structure seasonality than in systems regularly punctuated by seasonal abiotic events.

Within the wide diversity of systems considered, it is perhaps not surprising that no consistent patterns or trends are recognizable. One of the few possible regional generalizations relates to the limited influence of predation in controlling zooplankton populations in New Zealand (Chapman *et al.*, 1975). For the rest, seasonal responses largely reflect the specific attributes of particular systems. Why, for example, do ZSS maxima occur in winter in certain waters between 0° and 45° S, while summer biomass maxima characterize others within the same latitudes? Why are given species not necessarily consistent in their seasonal maxima (Bayly & Williams, 1973)? Answers to such questions can only be sought by consideration of site-specific events. Given the hydrological variability of arid and semi-arid regions (Alexander, this volume), and the susceptibility of tropical waters to aperiodic events, long-term studies are required to assess the considerable inter-annual variability which exists. Finally, multi-disciplinary studies are essential to unravel the ecological complexities involved. Studies of zooplankton in isolation are unlikely to help in progressing from the descriptive phase to one of analytical and predictive capability.

Temperature has been recognized as the primary correlate of seasonality in many studies. This proximate relationship provides little or no insight into the *causal* mechanisms involved. Unfortunately, it is not as simple to measure complex variables like the abundance, size distribution and biochemical composition of seston, or the magnitude and selectivity of predation, as it is to measure temperature *per se*.

Seasonality of zoobenthos

The zoobenthos of standing waters has received much less attention than the zooplankton, particularly in the Southern Hemisphere. Quantitative seasonal studies are especially inadequate, and were so even in the Northern Hemisphere as recently as a decade ago (Brinkhurst, 1974).

While many fast-growing benthic organisms exist, particularly within the Chironomidae, which are capable of exploiting transient events, the detritivorous feeding mode and large size of many others potentially prolong longevity, and reduce their seasonality in comparison with small organisms like zooplankters with short response-times. Detritus is thought to stabilize the carbon cycle of aquatic ecosystems by buffering short-term fluctuations in food resource (Saunders, 1972) and so provide detritivores with a more regular food supply. However, the zoobenthos ultimately relies upon allochthonous and/or autochthonous autotrophic production, the seasonal variation of which must influence the dynamics of this fauna.

The structuring of the food environment of the zoobenthos by physico-chemical events in Lake Esrom has been described by Jónasson (1978). His analysis, together with more general accounts (Mann, 1980a, b; Pomeroy, 1980) suggests the usefulness of differentiating between stratified and non-stratified systems in considering zoobenthos seasonality. Generally speaking, detritivorous zoobenthos survive on degraded organic matter, but grow and reproduce when seasonal injections of fresh food occur. In the profundal, low oxygen tensions may preclude the use of abundant detrital food resources during stratification (Jónasson, 1978). Thus stratification and its chemical and biological consequences will influence the zoobenthos temporally (Fig. 10).

Zoobenthos seasonality in thermally stratified environments

The limited information on the benthos of profundal sediments in low latitude and Southern Hemisphere lakes suggests a markedly impoverished profundal benthic fauna in comparison with temperate lakes. In Amazonian *várzea* lakes stratification and subsequent oxygen depletion of deeper

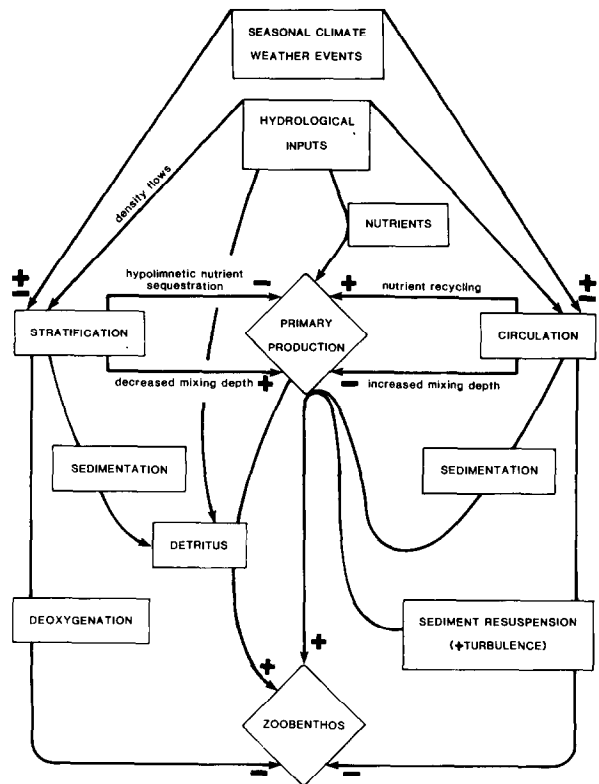


Fig. 10. A schematic model of physical and biotic factors influencing zoobenthos. This diagram should be considered in conjunction with principles relevant to zooplankton shown in Fig. 2.

waters occurs seasonally at high water levels. Only two chironomid species – a predator and its prey – tolerate these conditions. Even in shallow marginal waters, floating meadows limit circulation and the accompanying reduction in oxygen tension creates adverse conditions for the littoral fauna (Reiss, 1977).

Seasonal stratification and hypolimnetic oxygen depletion is a characteristic summer event in many man-made lakes e.g. Lakes Volta (7°N), Kariba (18°S) and McIlwaine (18°S). In these systems, the benthic fauna was depleted seasonally following the development of anoxic conditions in deeper waters, or did not occur in profundal sediments (McLachlan, 1970b; McLachlan & McLachlan, 1971; Petr, 1972; Kenmuir, 1980; Marshall, 1982). This contrasts sharply with the proliferation of zoobenthos in the anoxic profundal of temperate lakes, particularly eutrophic ones (Brinkhurst, 1974). The limitation of anaerobic benthic fauna in

low-latitude lakes may be ascribed to the elevated metabolic rates, low oxygen saturation levels and the high rate of oxygen depletion at high ambient temperatures. Fully saturated waters contain c. 11.3, 9.1 and 7.6 mg l⁻¹ oxygen at 10°, 20° and 30 °C respectively. Assuming depletion occurs simply at a Q₁₀ of 2, such waters would become anoxic after 100, 40 and 17 time units, respectively: prospects for faunal acclimation to decreasing oxygen tensions would be progressively shortened as temperatures rise. Organic matter does not readily accumulate in tropical waters in view of its rapid decomposition (McLachlan, 1974). Thus inadequate food supplies in the profundal probably also limit the fauna under stratified conditions when sedimentation is reduced (cf. Jónasson, 1978).

Zoobenthos seasonality in circulating waters

Zoobenthic communities in shallow, well-mixed waters are influenced by the stability of bottom sediments. Unconsolidated deposits tend to be inimical, as they are easily resuspended, smothering benthic organisms and frequently depleting oxygen levels in overlying waters. Organisms living on stable deposits escape these constraints, and are better able to benefit from the continued supply of organic matter fixed in the overlying euphotic zone. Benthos in the shallow littoral zone is influenced by wave-wash, regardless of the stability of the substratum, and tends to be susceptible to fluctuations in water level.

Lakes George (0°) and Chilwa (15 °S) have unstable muddy bottoms, that of the former being too liquid to support animals (Darlington, 1977). Its benthos is accordingly dominated by meroplanktonic chaoborid larvae, one species of which declined 3-fold during the rainy season, possibly as a result of emergence, while the other varied little between the rainy and dry seasons (McGowan, 1974). In a subsequent year when the rainy season was delayed, Darlington (1977) found no evidence of seasonal changes in abundance or composition of benthic invertebrates over the half-yearly seasonal cycle. Chironomid larvae dominated the benthos of Lake Chilwa, in which seasonal patterns were obscured by more severe changes in habitat – the drying out and re-inundation of this unstable environment (Kalk *et al.*, 1979). Its benthic fauna is

largely dependent upon inputs of organic matter from the *Typha* swamps fringing the lake, and much of the faunal biomass is associated with dead *Typha* leaves (McLachlan, 1979). The off-shore sediments of Chilwa support few benthic organisms: these tend to concentrate in a ring around the land-water interface, leaving vast off-shore areas devoid of benthic animals. Water level fluctuations dominate seasonal events in this system.

Lake Chad (13 °N) exemplifies another unstable ecosystem, which undergoes pronounced seasonal and longer-term fluctuations in level, and functions as a vast 'littoral' zone (Lévêque, 1979). The density and biomass of its benthic fauna varies seasonally in relation to changes in water temperature and depth (Lévêque, 1979) although it is not clear which of these factors exerts the greater controlling influence. Oligochaetes, chironomids and certain mollusc species were more abundant during the cool season, when water levels were high. The mobilization of new food resources by rising water levels may be primarily responsible for the increase in benthic biomass observed (e.g. McLachlan, 1974). Allochthonous material introduced by the floodwaters of the influent Chari River potentially enhances food supplies further.

Some seasonal studies of the littoral benthos of rather deeper systems exist. McLachlan & McLachlan (1971) concluded that the littoral fauna of Lake Kariba was little influenced by seasonal events, apart from the creation or inundation of new habitats (beach barrier pools) and changes in bank erosion and hence suspended sediment loads as a result of changes in water level. Colonization rates of wood substrata exposed *in situ* to simulate drowned trees were seasonally similar (McLachlan, 1970a), but major increases in biomass occurred at the shore edge as water levels rose. This was almost entirely due to rapid colonization by a pioneering chironomid (McLachlan, 1970b) exploiting the inundation of terrestrial organic matter (McLachlan, 1974). Similar colonization of flooded terrestrial vegetation was evident in Lake McIlwaine (Mars hall, 1982). In other situations, the density of slow-growing benthic organisms may appear to decline as water levels rise, simply as a result of dispersion into an expanding littoral habitat (e.g. the decapod shrimp *Caridina nilotica* (Roux) in Lake Sibaya (27 °S, Hart, 1981b), rather than in response to adversity. Conversely, falling water levels strand

less motile fauna, and impose a seasonal mortality with particularly significant consequences to benthic littoral fauna inhabiting reservoirs with pronounced drawdown, for example, Lakes Kariba (Kenmuir, 1980) and McIlwaine (Kenmuir, 1980; Marshall, 1982).

Rainfall is known to influence the population ecology of various aquatic snails. On the coast of Kenya, reproductive peaks of *Bulinus globosus* (Morelet) were recorded after heavy seasonal rainfall (O'Keeffe, in press), although the causal mechanism was not established. Expansion of habitat, provision of space and new food resources, or stimulation of periphyton production by nitrogen-enriched rainwater are possible reasons. Ironically, since intrinsic rates of population increase of this species declined above 28.5 °C, unseasonal rainfall during the cooler season was particularly favourable for the development of large populations. Lymnaeid snail populations which breed year-round in Queensland (Blair & Finlayson, 1981) are also influenced by rainfall which both inundates aestivating snails and washes animals away. In the Transvaal lowveld of South Africa, lymnaeids breed mainly in the dry cooler months (Appleton, 1974) and in doing so, they may avoid turbid conditions which are known to have deleterious effects on the egg capsules of planorbid snails (Harrison & Farina, 1965). Many studies have focussed upon the effects of temperature on the performance and dynamics particularly of disease-vector snails (Appleton, 1977; 1978).

Little numerical information is available in respect of the zoobenthos of Australian and New Zealand waters (Bayly & Williams, 1973; Forsyth, 1975; Winterbourn & Lewis, 1975). In Lake Werowrap (39 °S), fluctuations in density of *Tanytarsus barbitarsis* Freeman were attributable to emergence, available food, and predation by a dytiscid (Paterson & Walker, 1974). Populations of *Paratemia zietziana* Sayce were multi-voltine in Pink Lake and Lake Cundare (38 °S). Densities were extremely low in winter, and recruitment was unpredictable in respect of timing and cohort size (Marchant & Williams, 1977). Timms (1981) concluded that different factors structured the zooplankton, littoral and benthic fauna in saline Lakes Purrumbete, Bullenmerri and Gnotuk (39 °S), in which communities exhibited little synchrony despite their exposure to similar thermal régimes. The

abundance of benthic fauna in Great Lake and Arthur's Lake (42 °S) in Tasmania was related to fluctuations in water level (Fulton, 1983). On the other hand, some recurrent seasonal patterns have been noted (e.g. Williams, 1981).

Pupation and emergence patterns influence the abundance of benthic insect larvae. In a shallow bay of equatorial Lake Victoria, MacDonald (1956) noted marked rhythmic monthly oscillations in density of benthic chironomid and chaoborid larvae. The life-cycle periodicities of different species were roughly monthly or multiples thereof. Semi-synchronous pupation and emergence resulted in density oscillations suggestive of a lunar periodicity. Despite the thermal constancy of the site, the magnitude of monthly density peaks of *Chironomus* were seasonally variable, possibly reflecting the multi-specificity of this assemblage while those of *Tanytarsus guttatipennis* Goetgh. were seasonally uniform.

Lake Sibaya (27 °S) provides an example of a rather deeper, circulating system with a significant offshore zoobenthos. In contrast with the apparent decrease in benthic biomass with depth evident in stratifying systems, the infaunal crustacean benthos of Sibaya increased markedly below 20 m (Boltt, 1969; Hart, 1979). While the water column does not stratify, diel micro-stratification at the sediment-water interface during summer imposes a seasonal influence upon the vertical distribution of the fauna.

Zoobenthos seasonality in floodplain lakes

The benthic fauna of Amazonian *várzea* lakes is well adapted to fluctuations in water level, and migrates into or out of the various benthic biotopes as waters rise or recede (Reiss, 1977). High turbidity tends to limit the development of submerged plants. Floating meadows, the 'limnokinal' communities, and inundated forests therefore provide much of the organic matter and energy required to support the benthos. While some seasonality is imposed by alternate stranding and flooding of the biotopes, the major seasonal fluctuations in faunal abundance are related to changes in dissolved oxygen levels; faunal density and oxygen concentrations increase and decrease in a converse manner to seasonal changes in water level (Fittkau *et al.*, 1975). To what extent the low-water faunal increase is

attributable to crowding in a shrinking habitat is not clear.

Seasonal flooding is a major ecological event in the floodplain of the Pongola River (Heeg *et al.*, 1980; Heeg & Breen, 1982) whose pans are broadly analogous to the Amazonian *várzea* lakes. Zoobenthic biomass increased both in mid-pan sediments and littoral margins after summer inundation of marginal grasslands (Walley, 1979), seemingly in response to inputs of terrestrial detritus and that generated from the die-back of the winter growth of submerged macrophytes. Spatial variability within and between pans, as well as inter-annual differences obscured trends, but cool-season peaks were evident.

Seasonal growth of aquatic macrophytes which provide food and shelter promoted the development of a large and diverse macroinvertebrate fauna by the end of the rainy period in seasonally-flooded billabongs along Magela Creek (13 °S). Fauna fluctuations were greater in shallow than deep billabongs (Marchant, 1982), reflecting the greater capability of the latter to buffer environmental perturbations.

Some conclusions

The zoobenthos, like the zooplankton, does not possess a uniform seasonal pattern; given the diversity of situations considered, it is unrealistic to expect conformity. Many of the changes in abundance which take place coincide with variations in water level. The seasonality of these communities is accordingly intimately associated with hydrographic characteristics. In many cases, faunal abundance increases as water levels rise, probably as a consequence of improved feeding conditions and an expanding habitat. Experimental validation for these inferences is, however, lacking. The frequent increase of zoobenthos with a rise in water level contrasts with the decline observed in several zooplankton communities during the rainy season.

Dissolved oxygen levels also influence the benthic fauna markedly, and seasonal developments of reduced or anoxic environments impose corresponding spatio-temporal restrictions on the fauna. The rapidity with which oxygen depletion can occur at the higher temperatures of the lower latitudes accentuates the severity of this restriction.

Finally, it should be noted that while benthic organisms feature prominently in the diets of many

fish, little attention has been given to the undoubtedly significant rôle of predation in structuring benthic communities.

Seasonality of stream invertebrates

Benthic invertebrates, especially aquatic insects, exhibit very clear seasonal cycles in many temperate streams in the Northern Hemisphere (Hynes, 1970). Generalized stream ecosystem models derived principally from this regional data base (Vannote & Sweeney, 1980; Vannote *et al.*, 1980) imply that seasonally staggered development periods have evolved through interspecific competition and serve to optimize resource utilization. Increased niche differentiation consequent upon such resource optimization may have increased speciation. Assessments of the validity of these concepts in streams in New Zealand (Winterbourn *et al.*, 1981) and Australia (Lake, 1982) have suggested that regional differences in stream structure and function exist, particularly with regard to the nature and timing of allochthonous energy inputs, and to the hydrological régimes. Despite these differences, general determinants of seasonality are shared by stream fauna (Fig. 11).

The influence of temperature and photoperiod upon the seasonality of Northern Hemisphere stream fauna was recognized by Hynes (1970). Mechanisms of the thermal influence were explored for aquatic insects by Vannote & Sweeney (1980) who detailed bionomic and bioenergetic effects. Other physical factors, for example, in-stream current velocity (Chutter, 1969) and substratum stability in unstable zones (Chutter, 1970; Hurtle & Lake, 1982; Saenger *et al.*, 1982), are likely to vary seasonally with rainfall and ensuing stream discharge, affecting stream fauna. Cyclical or episodic meteorological conditions also influence food supplies, the nature and amount of which, along with temperature, co-determine the seasonality of filter-feeding aquatic insects (Wallace & Merritt, 1980).

Invertebrate seasonality in Southern Hemisphere streams

Erratic, variable rainfall patterns which typify most arid or semi-arid regions confer a corresponding variability in stream-flow characteristics (Alex-

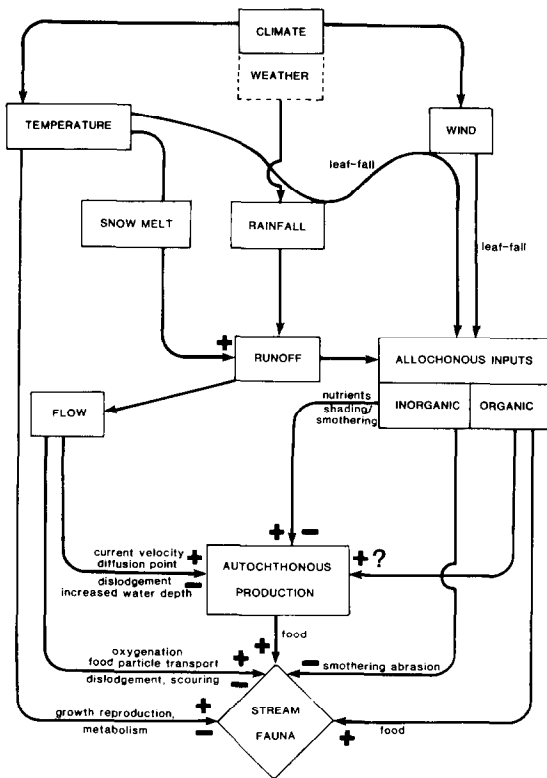


Fig. 11. A schematic model of environmental factors influencing stream invertebrates. Read in conjunction with Fig. 2.

ander, this volume), and streams are liable to stop flowing for shorter or longer periods, seasonally or aperiodically. Conversely, equable climates permit more uniform, perennial flow régimes. Relatively low timberlines in southern land masses (Winterbourn *et al.*, 1981) potentially reduce the significance of allochthonous energy inputs. Headwater reaches particularly, may therefore be autotrophic rather than heterotrophic as suggested by Chutter (1970). Leaf fall derived to a greater extent from deciduous trees rather than evergreen, with consequences upon the timing of such inputs, and possibly also upon its biochemical lability (e.g. King, 1981). Streams in Australia (Lake, 1982) and parts of South Africa (J. M. King, Univ. Cape Town, pers. comm.) receive the bulk of their allochthonous inputs during summer, in contrast with the strongly seasonal autumn input into north temperate streams. Empirical support for many of these suggested features of the trophic ecology of stream fauna is largely wanting, however.

Variable hydrological conditions would seem to

favour stream fauna with flexible or opportunistic life histories. Several studies have demonstrated a reduced seasonality of fauna in Southern Hemisphere streams (e.g. Hynes & Hynes, 1975; Towns, 1983). Nevertheless, some seasonality is evident (Chutter, 1970; King, 1981, 1983; Towns, 1983), and increased systematic knowledge has improved resolution of specific seasonal patterns (Towns, 1983). Studies on tropical streams are very scarce. In one of the few examples, fauna in tree-shaded creeks of the Amazonian *terra firma* which receive considerable allochthonous inputs, showed little seasonality (Fittkau *et al.*, 1975).

Faunal seasonality understandably reflects the environmental features which dominate a given system. In the upper Vaal River (c. 27°S; Fig. 1), Chutter (1970) distinguished three major biological seasons. In winter, river flow is low, and the water clear and cold. During the early summer, flows are still low and the water clear, but higher temperatures and longer daylengths potentially improve conditions for autotrophic production. In the rainy summer season, flows increase and episodic flooding occurs. Movement of silt and sand in the river bed disrupts the fauna and increases turbidity, reducing the potential for autotrophic production.

The fauna of each of three distinct zones in the 40 km long Eerste River (34°S) in the winter rainfall region of southern Africa, showed different seasonal patterns (King, 1981), apart from a shared numerical peak in spring in each zone (King, 1983). The 'winter' communities whose life cycles began in winter, appeared almost simultaneously with the winter rains, and predictable seasonal changes occurred at the same time each year (King, 1981). Faunal size distributions were similar before and after catastrophic floods leading King (1981) to suggest that the stream fauna persisted by migrating into and out of deep stream sediments in response to unpredictable flows. The biomass of macroinvertebrates in the Eerste River was considerably lower than that recorded in streams receiving deciduous leaf inputs. King (1983) attributed this partly to the seemingly decay-resistant nature of the allochthonous detritus entering this river, and partly to the depopulating effects of its episodic spates. In addition, many species emerged in summer, possibly to avoid high temperatures, leaving the major summer energy input largely unexploited (J. M. King, pers. comm.).

It has been suggested that stream fauna in Africa,

Australia and New Zealand is controlled primarily by the physical environment (Chutter, 1970; Winterbourn *et al.*, 1981; Lake, 1982; Towns, 1983) and only secondarily by biotic factors. The flexible life cycles observed appear adaptive both to the unpredictable conditions of Africa and Australia, as well as to the mild climate of New Zealand (Towns, 1981). Long periods of diapause provide protection against drought, or against stagnant low-water conditions which are inimical for current-dependent species or stage. For insects, extended hatching and emergence periods enhance the chances for both aquatic and aerial life history stages to encounter favourable periods within their unpredictable and variable environments (Lake, 1982). The life-histories of non-insect fauna are also well adapted to environmental conditions. For instance, the seasonal breeding peak of the shrimp *Paratya australiensis* Kemp coincides with low-flow conditions, minimizing downstream losses of its planktonic larvae (Williams, 1977).

Bark and branch litter, which falls continuously throughout the year, and decomposes slowly in water compared with leaves, contributed most allochthonous biomass and energy to a temperate Australian creek (Blackburn & Petr, 1979). In New Zealand streams, fine particulate organic matter probably provides a more continuous and less limited supply of food for stream fauna than more strongly seasonal inputs of coarse leaf-litter (Towns, 1983). A greater continuity in supply of allochthonous inputs reduces the need for faunal life cycles to be synchronized to seasonal energy pulses. The resulting opportunity for greater life-history flexibility is obviously advantageous in the face of unpredictable hydrological and related physical conditions. Stream communities are nonetheless sometimes ravaged by abiotic events. Subsequent recolonization by immigrant flying insects (Winterbourn *et al.*, 1981), or possibly by migration from deep sub-stream sediments (King, 1981), is important in the perpetuation of stream communities living in unpredictable environments.

The influence of fish predation upon stream fauna has been poorly studied, but Lake (1982) noted that all Australian stream fish were either macro-invertebrate predators or piscivores, and inferred that they would exert considerable predation pressures on stream benthos.

Some conclusions

The Southern Hemisphere stream fauna has been poorly studied, particularly in the tropics. There is evidence that life histories are more flexible and opportunistic, either in response to unpredictable, or to mild, uniform environmental conditions, in Southern than Northern Hemisphere stream fauna. Inferences on trophic ecology suggest significant departures from the north temperate 'norm', but empirical observation is lacking.

Seasonality of faunal production

Production, turnover rate or energy flow estimates provide better insight into the dynamics of faunal populations than static measures of abundance. However, since relatively few estimates of these variables exist for Southern Hemisphere aquatic invertebrates, consideration of the seasonality of production *per se* is restricted. Crude inferences on production can be drawn from temporal changes in standing stock, which at least in certain zooplankton populations at lower latitudes (see below), appear to reflect changes in production. However, since production estimates are frequently derived from measurements of standing stock, the temporal concordance between these non-independent variables may be spurious. At best, changes in biomass can provide only crude insights into the temporal trends of production, and provide little or no insight into its magnitude.

Zooplankton

Apart from the studies on New Zealand calanoids (Green, 1976; Burns, 1979) there appears to be reasonable or good coincidence between seasonal changes in zooplankton production and biomass. This was evident for *Thermocyclops hyalinus* in Lake George (Burgis, 1971, 1974), the herbivorous and carnivorous zooplankton in Lake Lanao (Lewis, 1979), the zooplankton in Lake Chad (Gras & Saint Jean, 1983), *Pseudodiaptomus hessei* (Mrázek) in Lake Sibaya (Hart & Allanson, 1975) as well as both *Daphnia carinata* (King) and *Simocephalus exspinosus* (Kock) in Gumeracha oxi-

dation ponds (Mitchell & Williams, 1982a). Seasonal production and biomass changes were less closely related in *Calamoecia lucasi* and *Boeckella dilatata* in Lakes Ototoa and Hayes, respectively (Green, 1976; Burns, 1979).

Biomass turnover coefficients (P/B ratios) of zooplankton were directly correlated with temperature (and thus season) in Lakes Chad (Gras & Saint Jean, 1983), Sibaya (Hart & Allanson, 1975), Ototoa (Green, 1976) and Hayes (Burns, 1979), but poorly so in Gumeracha sewage ponds (Mitchell & Williams, 1982a), which are nutritionally rather artificial and dominated by a cold stenothermal daphnid.

Production and P/B values are also related to food availability, both within and between years. For example, during the annual cycle in Lake Ototoa, the P/B value of *C. lucasi* was positively related to food availability above 15 °C; i.e. outside the winter/early spring period. Green (1976) suggested that the specific growth rate of this calanoid was controlled jointly by food and temperature above 15 °C, and by temperature alone below 15 °C. A negative relationship between P/B and food abundance for *B. dilatata* above 8 °C in Lake Hayes was possibly artificial (Burns, 1979). Inter-annual variability in production and P/B values was apparent in Lake Chad where accelerated development times and increased fecundity were evident within zooplankton during years of low water level when food supply apparently improved (Gras & Saint Jean, 1978, 1981, 1983).

Continuous year-round breeding occurs in many zooplankters from the African tropics and subtropics (e.g. Burgis, 1971, 1973, 1974; Hart, 1981a) to the temperate latitudes of New Zealand (e.g. Chapman, 1973; Green, 1976; Burns, 1979, 1981). The latter examples emphasize the moderating influence of New Zealand's maritime climate upon seasonality (Jolly & Brown, 1975). Species showing continuous breeding exhibit seasonal variations in demographic attributes such as female size and its frequent correlate, clutch size, as Table 2 shows. These variations tend to increase with latitude, although the trend is disrupted. For example, in relative terms, the smallest and greatest annual variations in average clutch size were evident at similar latitudes (27° and 30 °S; Table 2). Bayly (1962) suggested that body size and clutch size were interactively determined by the rate of water renewal, temperature and food availability during development; factors which are not necessarily independent. Several of the studies cited above demonstrate inverse relationships between temperature and female size, and positive correlations between female size and clutch size. Food availability, along with temperature, has been shown to influence clutch size in *Boeckella symmetrica* Sars (Woodward & White, 1981) and *Metadiaptomus meridianus* (Van Douwe) (Hart, unpublished). Such influences have an important bearing on production, as in Lakes Roturua and Rotoiti, where Chapman (1973) noted the controlling influence of egg stocks on production.

Table 2. Absolute and relative annual ranges in female body length and clutch size of copepods in southern lakes, as a function of latitude. The relative value is the range difference as a percentage of the minimum value.

Species	Lake	Latitude	Body length (μm)		Clutch size		Authority
			range	%	range	%	
<i>Thermocyclops hyalinus</i>	George (Central)	0°			5 - 9.4	88	Burgis (1971)
<i>Pseudodiaptomus hessei</i>	Sibaya	27 °S	430- 480	12	18 - 24.4	35	(Hart (1981a)
<i>Metadiaptomus meridianus</i>	le Roux	30 °S	1 100-1 600	45	10 -120	1 000	Hart <i>et al.</i> (1983)
<i>Calamoecia lucasi</i>	Ototoa	36 °S	550- 590	7	1.3- 2.1	60	Green (1976)
<i>Boeckella propinqua</i>	Oroarotamahine	37 °S	1 386-1 760	27	3.3- 11.7	251	Bayly (1962)
<i>Boeckella dilatata</i>	Hayes	45 °S	770- 940	22	1.9- 7.3	284	Burns (1979)

Zoobenthos

Quantitative data on zoobenthos production is extremely limited. In the littoral of Lake Sibaya the biomass of an atyid shrimp was rather stable over about 10 months while production varied seasonally (Hart, 1981b). By contrast, production of the offshore benthic infauna of this lake was comparable in summer and winter (Bolt, unpublished, in Hart, 1979). Production and biomass changes in *Tanytarsus barbitarsis* were generally coincident in saline Lake Werowrap (Paterson & Walker, 1974), although P/B values (and recruitment rates) of consecutive cohorts of *Parartemia zietziana* were variable in other saline lakes (Marchant & Williams, 1977), possibly reflecting the unpredictability of its habitat. Spatial variation in P/B coefficients of the benthic fauna of Lake Chad have been reported (Lévêque, 1979), but the lack of contemporaneous records of production and biomass precludes an assessment of the seasonality of production. The benthic studies of Lake Chad are especially valuable in providing concurrent data on community energetics.

Production of the oligochaete *Branchiura sowerbyi* Beddard in some Pongola pans was strongly seasonal (Walley, 1979) and closely followed seasonal changes in abundance, but as noted above, caution is required in interpreting concordance between production and biomass.

Some conclusions

Little is known concerning the seasonality of production in Southern Hemisphere aquatic invertebrates. Several examples of apparent correspondence between temporal changes in standing stock and production in zooplankton in lower latitudes ($<35^\circ$) imply that fluctuations in abundance may crudely reflect temporal trends in production. These examples point to the attainment of a closer dynamic stability between organisms and their resources in less markedly seasonal environments than may be possible under conditions of pronounced seasonality, where the correspondence is weaker.

Several benthic and planktonic animals breed perennially under the warmer conditions of the lower latitudes, with significant bioenergetic consequen-

ces. Young, growing animals generally return a higher net production efficiency ($K_2 = \text{production/assimilation}$) than sexually mature individuals, largely because of their lower *absolute* metabolic costs (Calow, 1977). The continued presence of numerous young individuals can influence the population K_2 efficiency favourably, improving production per unit of assimilated energy, and elevating the population P/B ratio, as exemplified for *Caridina nilotica* (Hart, 1981b; Hart & Allanson, 1981). Aquacultural implications are considerable.

Concluding remarks

The Southern Hemisphere data base is comparatively poor by Northern Hemisphere standards, but except under particular localized conditions, existing studies provide little support for the notion of aseasonality. Seasonal fluctuations in standing stock tend to become more pronounced with latitude, although within the zooplankton this trend is neither uniform, nor consistent (Fig. 4), partly as a result of differences in stability linked to continentality for example.

Patterns of seasonality are difficult to discern at the level of analysis presently feasible. The great diversity of aquatic ecosystems considered is broadly mirrored in the diversity of faunal responses, and faunal seasonality is predominantly determined and driven by the specific characteristics of the particular ecosystem. In general though, a considerable body of circumstantial evidence supports the notions of Talling (1966), Beadle (1974) and others that seasonal variation in wind or precipitation becomes the major driving variable of temporal events in low-latitude lakes.

Overt faunal seasonality obviously reflects the populations' integrated response to a wide array of interacting biotic and abiotic factors. Fundamental advances in the exploration of the precise mechanisms underlying these interactions are needed. Broad ecological/limnological principles developed in northern temperate waters are obviously global in application, but require qualitative fine-tuning on the basis of regional limnological peculiarities. The predominance of elevated temperatures, monomictic/polymictic mixing patterns, the effects of inorganic suspensoids, and the erratic and variable flow régimes are specific limnological issues which

require particular consideration in the context of Southern Hemisphere waters.

Future studies should attempt to advance by a 'quantum jump' from the purely descriptive to the analytical. The spatio-temporal distribution of faunal populations represents their integrated responses to a complex of biotic and abiotic factors interacting with feedback. Given the considerable inter-annual variability which exists, and the less predictable characteristics of low-latitude waters, long-term studies are especially called for, as has been recognized repeatedly in the past. Broad-based, holistic studies are generally necessary to provide the quantitative understanding necessary to unravel the ecological complexities involved.

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